52. On the External Characters of the Beaver (*Castoridæ*) and of some Squirrels (*Sciuridæ*). By R. I. Pocock, F.R.S., F.Z.S.

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(Text-figures 38–60.)

Contents.

	Page
Introduction	1171
The Muzzle, Mouth, and Facial Vibrissæ	1173
The Ear	1177
The Feet	1183
a. Feet of the Tropical Asiatic Squirrels	1184
b. Feet of the Tropical African Squirrels	1188
c. Feet of the European and American Squirrels	1190
d. Feet of the Chipping Squirrels	1193
e. Feet of the Bristly Ground Squirrels	1195
f. Feet of the Sousliks and Marmots	1198
g. Feet of the Flying Squirrels (Petauristidæ)	1200
h. Feet of the Beaver (*Castor*)	1205
The Anus and External Genitalia	1208

Introduction.

The Squirrels, Marmots, and other admittedly related genera forming the Sciuridæ were formerly associated with the Beavers, or Castoridæ, in a primary division of the Simplicidentate Rodents, the Sciuromorpha[*]. It has become the fashion in recent years to drop this group. Nevertheless, the two families are still suggestively juxtaposed by systematic writers, and no one seems to doubt the validity of the claim of their relationship based upon certain cranial characters connected more particularly with the structure of the zygomatic arch. Miller, for example, in his key to the families of Rodents of Western Europe, places the Castoridæ and Sciuridæ under a heading distinguished from the other families by having the anterior portion of the zygomatic arch formed chiefly by the jugal bone and the infraorbital foramen small; and the opening words of his diagnosis of the family Castoridæ are "characters essentially as in the Sciuridæ." Alston, Thomas, Flower, Tullberg, Winge, Max Weber, and others all agree in placing the Castoridæ and Sciuridæ in the same section of Rodents.

As regards the division of the Sciuridæ into subfamilies there has been, and is still, some difference of opinion. By most authors the Marmots and Sousliks were separated as a subfamily —*Arctomyinæ* (*Marmotinæ*)—from the Squirrels (*Sciurinæ*); but

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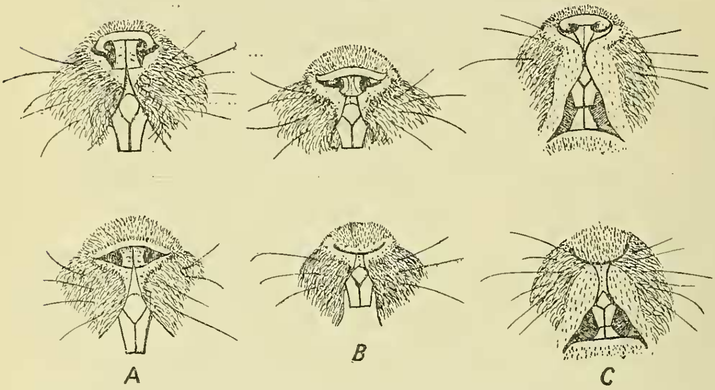
[*] Also containing the Aplodontidæ, about which I have no first-hand knowledge. This family was, however, removed from the Sciuromorpha by Thomas, P. Z. S. 1896, p. 1015.

Forsyth Major and Miller withheld that rank from them. On the other hand, the Flying Squirrels, which were usually distinguished as the subfamily *Pteromyinæ* (*Petauristinæ*), were granted by Miller the full family rank as Petauristidæ, equivalent to the rest of the Squirrels or Sciuridæ. A fourth subfamily—*Nannosciurinæ*—admitted as valid by some authors, was shown by Thomas in 1915 * to be composed of heterogeneous elements, the evidence of affinity between the genera derived from skulls being entirely untrustworthy.

The question of the generic classification of the Sciuridæ need not be discussed at length. All that it is necessary to say is that in 1915 Thomas clearly showed, by his study of the *os penis* or *baculum*, that previous attempts to affiliate the genera and subgenera by their skulls and teeth and other characters had in many instances yielded erroneous results, such as association of *Callosciurus* with *Sciurus* and of *Nannosciurus* with *Myosciurus*. No living student of the family would claim that we know the relationship of all the groups of genera to each other. The vagueness and diversity of opinions on this point, coupled with the hope of finding unrecorded features of systematic value, induced me to take up the study of the external characters presented by the ears, feet, and other organs which had been for

Text-figure 38.



A. Muzzle of *Sciurus vulgaris*, with rhinarium exposed and partially concealed by hood.

B. The same of *S. saltuensis*, with rhinarium exposed and entirely hooded.

C. Ditto of *Geosciurus capensis*.

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* Ann. & Mag. Nat. Hist. (8) xv. p. 386.

the most part neglected by previous workers, partly owing to scarcity of materials, either fresh or preserved in alcohol, suitable for the purpose. The result of my observations, extending over many years and based upon specimens that died in the Zoological Gardens, form the subject-matter of the present paper. Examples of a good many genera have passed through my hands in that way; but in some cases I have been compelled to rely upon dried skins contained in the collections of the Zoological Society and of the Natural History Museum *.

The Muzzle, Mouth, and Facial Vibrissæ.

The muzzle in all the genera of Sciuridæ and Petauristidæ is very uniform in structure. A peculiarity of the rhinarium is the mechanism by which the nostrils are closed. The hairy skin of the muzzle just behind it on the dorsal side is capable of being moved downwards and forwards, carrying the supranarial portion of the rhinarium with it, the two constituting, as it were, a kind of hood or cap over the nostrils. When completely lowered, the inferior edge of this hood forms a transverse or crescentically curved line defined from the upper lip by a narrow slit of the same shape. The line along which the upper half of the rhinarium is folded down is usually, at all events, marked by a transverse groove just above the upper edge of the nostrils. The rhinarium itself is naked and has a well-marked median groove between the nostrils, which are of the usual shape, with the typical narial slit behind and externally, and the expanded orifice in front and internally. They are moderately widely separated and look straight forwards. The rhinarium varies somewhat in shape. For instance, in *Sciurus vulgaris* it is comparatively deep, and has a nearly straight or convexly rounded upper edge. In *Sciurus saltuensis* it appears to be lower with the upper edge not nearly so raised. It also appears to be broader and altogether larger relatively in *Marmota* than in *Cynomys*. But although these observations were made upon fresh specimens, the apparent height of the rhinarium varies so much in accordance with the expansion or contraction of the hood, that I have found it impossible to make any useful systematic generalisations with regard to its shape. (Text-figs. 38 & 39, A–C.)

The two halves of the upper lip are completely divided up to the inferior median point of the rhinarium.

The rhinarium in *Castor* is very different from that of the Squirrels. The nostrils are widely separated, look outwards and upwards and are valvular, closing to form a crescentic slit. The area around them is naked, and the wide naked internarial space has an oblique crest of hairs passing over the nostrils on each side, and there is an upstanding crest on each side of the front of the infranarial portion of the rhinarium. The rhinarium is not mesially grooved and the upper lip is not cleft, although the short hairs on each side of the middle line are inclined inwards and downwards in a different direction from those external to them and form a definite crest or fringe. (Text-fig. 40, A, B.)

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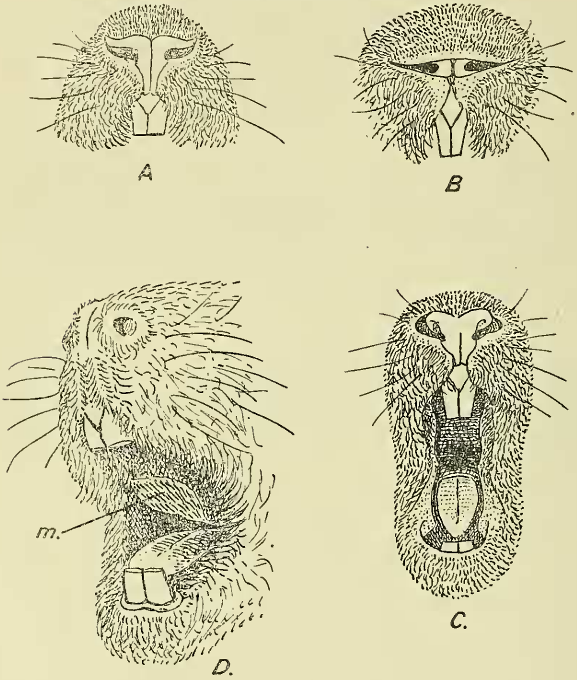
* I have to thank Mr. Oldfield Thomas not only for permission to examine the collections under his charge, but also for much kind help in the identification of some of the species of this difficult group about which I was in doubt.

The *mouth* in Sciuridæ and Petauristidæ is provided with two palatal lobes of hairy integument jutting inwards from the cheek. These are capable of meeting over the palate behind the incisor teeth, but they are never fused in the middle line. Two similar but smooth and altogether smaller lingual lobes jut inwards on each side of the tongue. (Text-fig. 39, C.)

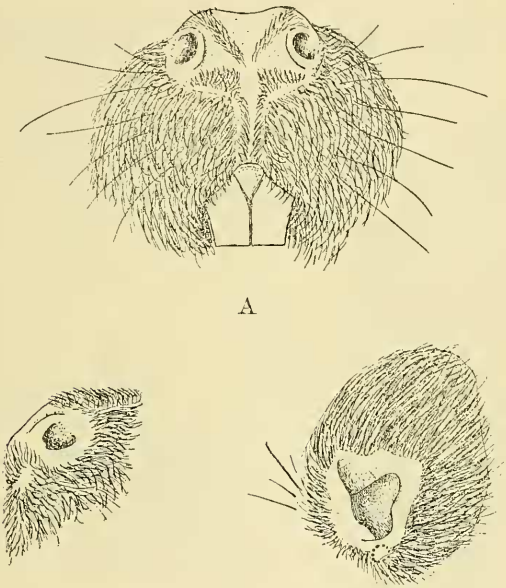
Text-figure 39.



A. Muzzle of *Cynomys ludovicianus*, with rhinarium exposed.
B. ,, ,, *Ratufa indica*, with rhinarium partially hooded.
C. Mouth and muzzle of *Marmota marmota*, showing the cheek-lobes projecting into mouth, and rhinarium exposed.
D. Mouth and muzzle of *Castor canadensis*, half side view, to show mat of bristles (*m.*) inside the cheek.

Definite cheek pouches are developed only in three genera—*Tamias* (*Eutamias*), *Citellus*, and *Cynomys*. I have not been able to examine them in *Citellus*, but in *Tamias* and *Cynomys* they open into the mouth approximately on a level with the anterior end of the molar teeth. In *Tamias* they are of large size, and, when unstretched, reach back as far as the ear. In *Cynomys* they are much smaller and do not reach beyond the eye. Judging from the descriptions of the pouch of *Citellus* as "large," I presume it resembles that of *Tamias* and *Eutamias*. *Marmota* is usually described as being without cheek pouches, and I failed to find a trace of them in the typical European species *M. marmota*. Nevertheless, in his diagnosis of the genus, Miller says "cheek pouches rudimentary or absent." Elliot [*] describes them as small in the American species, assigned to *Marmota*, and Cory [†] cites their presence as a character of the subfamily *Marmotinæ*. (Text-fig. 41, C, D.) Fresh information is clearly wanted on this point.

Text-figure 40.



A. Muzzle and rhinarium of *Castor fiber*.
B. Rhinarium of the same from the side.
C. Ear of *Castor fiber*, with position of orifice dotted in.

In its palatal and lingual lobes the mouth of *Castor* resembles that of the Sciuridæ, but it differs in having a large pad on each side of the cheek, lying farther within the mouth than the normal lobes. Each of these pads is provided with stiff, short hairs, forming a kind of mat, and projecting downwards and backwards. The hairs of these pads meet in the middle line over the tongue in front of the molar teeth, and close the orifice of the throat. (Text-fig. 39, D.)

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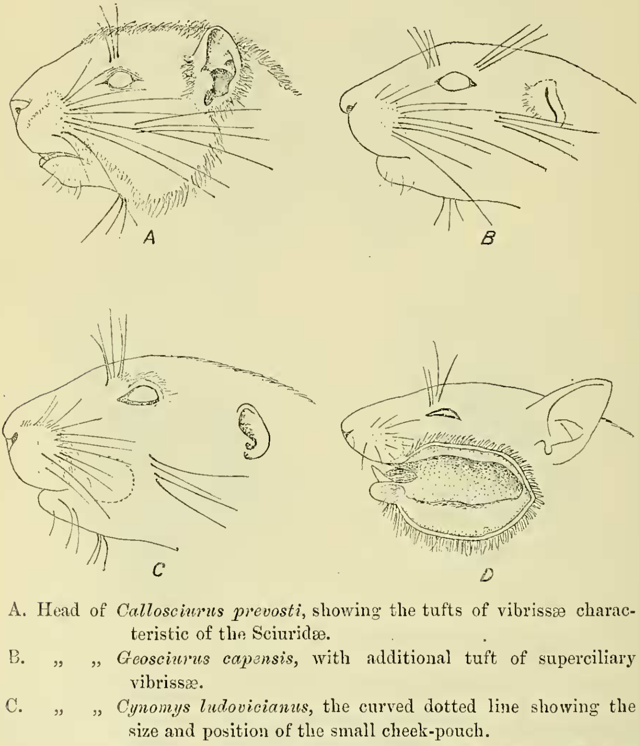
[*] Field Columbian Museum, Zool. ii. p. 104, 1901.
[†] 'The Mammals of Illinois and Wisconsin,' p. 137, 1912.

The tufts of the facial vibrissæ in all the genera of true Squirrels, in the Sousliks and Marmots are normal in number and position, the mystacials, supercilaries, and genals being long and comparatively numerous and the interramals, though less evident, being always detectable. The only variations to record are the absence of the interramal tuft in the Flying Squirrels (Petauristidæ) and the presence in the Bristly Ground Squirrels (*Xerus* and its allies) of a supplementary superciliary tuft of long vibrissæ over the posterior angle of the eye. In this particular these Ground Squirrels are unique, so far as I know, amongst mammals. (Text-fig. 41.)

Text-figure 41.



A. Head of *Callosciurus prevosti*, showing the tufts of vibrissæ characteristic of the Sciuridæ.
B. „ „ *Geosciurus capensis*, with additional tuft of superciliary vibrissæ.
C. „ „ *Cynomys ludovicianus*, the curved dotted line showing the size and position of the small cheek-pouch.
D. „ „ *Eutamias quadrivittatus*, with the external wall of the large cheek-pouch cut open.

The Beavers have a few short, stiff mystacial and superciliary vibrissæ, but the genal and interramal tufts are absent. In the absence of the genal tufts the Castoridæ differ from the Sciuridæ and Petauristidæ.

The systematic results yielded by the characters discussed may be tabulated as follows :—

a. Rhinarium unhooded, not wholly naked, nostrils wide apart, lateral, valvular; upper lip uncleft; mouth with a bristly pad inside the cheek ; no genal vibrissæ .... *Castoridæ*.
a′. Rhinarium hooded, *i. e.* capable of being covered by a flap of skin from the upper surface of the nose, naked, nostrils close together, looking forwards, not valvular; upper lip deeply cleft to rhinarium ; mouth without bristly pad inside cheek ; genal vibrissæ present .... *Sciuridæ* & *Petauristidæ*.
  b. Two tufts of superciliary vibrissæ, an anterior and a posterior. *Xerus* and its allies.
  b′. Only the normal anterior tuft of vibrissæ present.
    c. Interramal tuft of vibrissæ present .... *Sciuridæ* (including *Xerus*).
    c′ Interramal tuft of vibrissæ absent .... *Petauristidæ*.

The Ear.

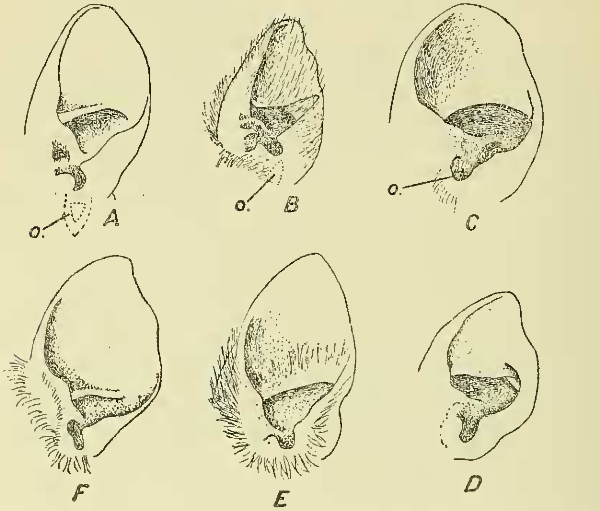
In the arboreal Squirrels the ear exhibits no marked structural variations. That of *Sciurus vulgaris* may be described as typical. It is oval in shape and stands away from the head from a point in front about on a level with the supratragus, and behind from a point below the antitragus. The anterior edge is folded over from the summit or tip of the ear, and the overfolded rim increases in thickness down to the supratragus. Beneath the supratragus the edge runs obliquely downwards and backwards into the cavity of the ear, and ceases on its inner wall about midway between the supratragus and the orifice of the ear. The orifice lies at the bottom of the cavity just below the level of the intertragal notch, which is defined in front by a small hemispherical tragus and behind by a large angular antitragus. The latter fits over the tragus when the ear is closed, and posteriorly is continuous with a large flap resulting from the overfolding of the posterior rim from a point a little above the line of the supratragus. The supratragus is a ridge with sharply defined inferior and poorly defined superior edge. It forms the upper border of the cavity of the ear, separating it from the feebly hollowed upper portion, which in height exceeds the height of the cavity. (Text-fig. 42, A.)

Judging from dried skins and material preserved in spirit, the ears of the American species *S. hudsonicus*, *carolinensis*, *niger* (*rufiventer*), *griseus*, *saltuensis*, *hypopyrrhus* and of several forms related to the last, resemble in all essentials those of *S. vulgaris*. So also do the ears of *Eutamias*, and of the Petauristidæ of the genera *Glaucomys*, *Eoglaucomys* and *Petaurista*, with the exception that in those Flying Squirrels the pinna is still more extended above the supratragus and the anterior edge is not overfolded to the summit. (Text-fig. 42, B, E, F.)

The ears of the Tropical Asiatic and African arboreal Squirrels differ from those of *Sciurus vulgaris* and of the American species above referred to in being shorter as compared with their antero-posterior width, in being less tubular at the base, so that the auditory orifice opens approximately on a level with the intertragal notch; the tragus and antitragus, especially the latter, are, on the whole, less well developed, and the summit of the ear does not project so high above the level of the head, although in *Ratufa* and *Funambulus* it is in this respect intermediate between the ears of *Sciurus vulgaris* and its allies and those of *Callosciurus* and *Funisciurus*.

In *Ratufa* (text-fig. 42, C) the ear rises from the head at a point about on a level with the anterior end of the supratragus in front and below the upper end of the antitragal thickening behind; its upper edge is rounded, not pointed, and the edge of the anterior margin is overfolded from the summit. Inferiorly the overfolded edge is continued downwards and backwards into the cavity of the ear, ceasing near its middle. Beneath its termination there is a shallow pit concealed within the antitragal thickening, which is low and not produced. There is no tragus, and the auditory orifice is just exposed within the intertragal notch. In *Callosciurus prevosti*, *C. notatus*, and *Tomeutes vittatus* the ear is less prominent than in *Ratufa*, and its points of attachment to the head in front and behind are somewhat higher. In *C. prevosti* also its upper portion is narrower and more pointed. In *C. vittatus* and *C. notatus* the posterior edge

Text-figure 42.



A. Ear of *Sciurus vulgaris*.
B. „ „ *Eutamias quadrivittatus*.
C. „ „ *Ratufa indica*.
D. Ear of *Funambulus palmarum*.
E. „ „ *Eoglaucomys fimbriatus*.
F. „ „ *Glaucomys volans*.
o., position of orifice.

(These figures are intentionally drawn of approximately the same size.)

is slightly emarginate above. In these three species the tragus is small or absent. (Text-fig. 43, A, B.) In *Funambulus tristriatus* the ear does not appear to differ in any essential points either in structure or relative size from that of *C. notatus*; but in *F. palmarum* it is less hairy and relatively considerably larger and has the posterior edge markedly emarginate above*. (Text-fig. 42, D.)

In the African Squirrels, *Funisciurus leucostigma* and *F. cepapi*, the ears are small as in *Callosciurus*, and do not appear to differ from them, although the cavity is perhaps more subdivided by hollows and low ridges; but in *Heliosciurus punctatus* the antitragus is better developed, being provided with a very definite process; the tragus is a curved, soft ridge, and the orifice of the ear, normally concealed by the antitragus, is narrowed and pointed above instead of being subcircular as in *Funisciurus*. (Text-fig. 43, C, D.)

The ears of the *Citellus*, *Cynomys*, and *Marmota* are mostly smaller than in the typical Squirrels; but within the limits of the genus *Citellus* the variation in size is considerable. In *C.* (*Otospermophilus*) *beecheyi* they are indeed relatively larger than in *Callosciurus* or *Funisciurus* and project above the level of the head; but in other species, *i. e.* some of those referred to the subgenus *Ictidomys*, they have been described by Allen as "generally small, sometimes rudimentary." Nevertheless, even in *C. beecheyi* they differ structurally from the ears of all the typical Squirrels examined. The cavity of the ear, bounded above by the supratragus, is to a considerable extent filled in front by a thickened development of the inferior continuation of the overturned anterior margin of the pinna; and this thickening is covered closely with longish hair covering the cavity and closing it when the ear is folded. There is no trace of tragus or antitragus, the lower rim of the cavity forming an evenly curved line. For the rest, the area above the supratragus is well developed and has a very distinctly emarginate posterior border; the tip is somewhat pointed, and the overfolding of the edge of the anterior rim does not quite reach the summit. In front the ear rises from the head at a point a little above the anterior end of the supratragus, and behind the posterior border fuses with the integument of the head just below the posterior end of that ridge. (Text-fig. 44, D.)

In *Marmota marmota* the ear is a little more reduced in size than in *C. beecheyi*, and the area above the supratragus is wider in proportion to its height; the tip is pointed, but the posterior border is less markedly emarginate. The points of origin of the free portion in front and behind are approximately at the same levels as in *C. beecheyi*; the cavity is similarly blocked in front by the hairy thickening of the injutting portion of the inferior continuation of the overfolded portion of the anterior rim, and there is no trace of tragus, antitragus, or intertragal notch. (Text-fig. 44, E.)

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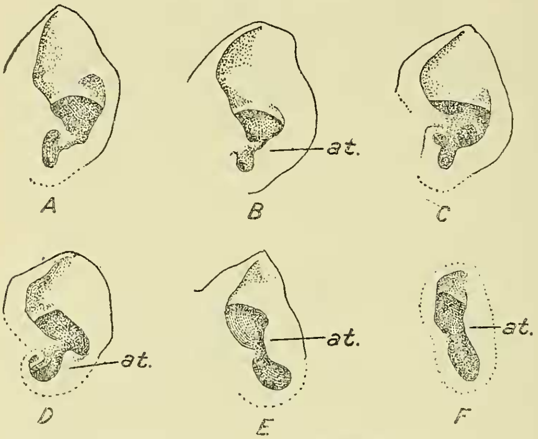
* Judging from dried skins the ears of *Tomeutes* seem to be like those of *Callosciurus*; but in the remarkable Bornean genus *Rheithrosciurus* these organs differ from those of the other Oriental genera in their great length. In this respect they surpass the ears of *S. vulgaris*; but details of their structure could not be determined on the made-up skins in the Natural History Museum.

In *Cynomys* the ear is very much smaller than in *Marmota* owing to the reduction in size of the area above the supratragus. The summit is rounded, and has its edge overfolded in continuation of the overfolding of the anterior edge. The hairy thickening projecting backwards into the cavity of the ear above the orifice is well developed, there is no tragus or intertragal notch, and at most a trace of antitragal thickening. (Text-fig. 44, F.)

In the Ground Squirrels of the genus *Xerus* and its allies, which are as terrestrial in their habits as the Sousliks and Marmots, the ears are greatly reduced in size, in some cases, indeed, *e. g.* in *Geosciurus capensis*, equalling apparently in that respect those of some of the small-eared species of *Citellus*. But they are modified for terrestrial life on quite a different plan from that exhibited by the Sousliks and Marmots.

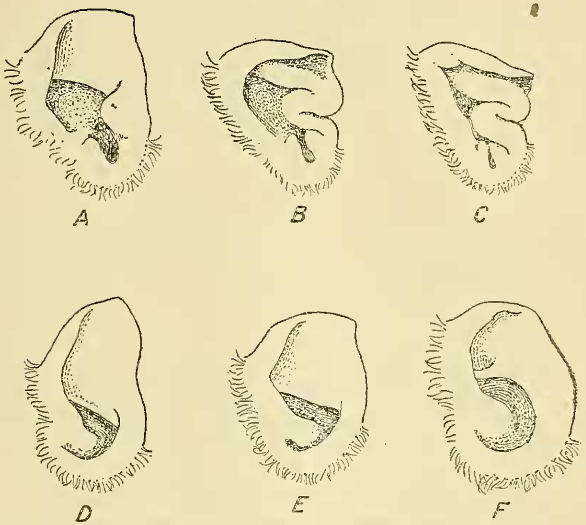
Text-figure 43.



A. Ear of *Callosciurus prevosti*.
B. „ „ *Tomeutes vittatus*.
C. „ „ *Funisciurus cepapi*.
D. Ear of *Heliosciurus punctatus*.
E. „ „ *Atlantoxerus getulus*.
F. „ „ *Geosciurus capensis*.
at., antitragal thickening.

In *Euxerus erythropus*, for instance, a comparatively large-eared form, in which the summit of the ear reaches about as high as the level of the head, the antero-superior and posterior margins meet approximately at a right angle. The anterior edge is overfolded, and is continued beneath the supratragus, where it bends backwards and downwards, ceasing just above the tragus, or sometimes running thence backwards and upwards as a rod-like ridge to the posterior end of the supratragus. The tragus is a hard, rounded eminence, and the intertragal notch is very deep. The antitragus is a thick bulging swelling set high above the tragus just beneath the posterior end of the supratragus, which fuses with it. The anterior edge rises from the head at a point about on a level with the anterior end of the supratragus and the posterior edge, which is nearly straight or slightly sinuous, from a point about on a level with the lower portion of the antitragal prominence. When the ear is closed the upper portion folds down on the supratragus, the antitragus is folded on itself and pulled forwards over the tragus, and with the supratragus blocks the upper part of the cavity, the intertragal notch at the same time being closed by the juxtaposition of its anterior and posterior walls. Thus the mechanism for closing the ear is quite different from that of the Marmots and Sousliks, where the supratragus is depressed against the hairy thickening invading the fore part of the ear-cavity, the thickening itself being pressed down over the orifice. Judging from a dried skin, the ear of *Xerus rutilus* is relatively a little smaller than in *Euxerus erythropus* owing to the reduction in size of the portion above the supratragus. (Text fig. 44, A–C.)

Text-figure 44.



A, B, C. Ear of *Euxerus erythropus*, in three stages of folding.
D. Ear of *Citellus* (*Otospermophilus*) *beecheyi*, from a dried skin.
E. ,, ,, *Marmota marmota.*
F. ,, ,, *Cynomys ludovicianus.*

In *Atlantoxerus getulus* the ear seems to be relatively a little smaller than in *E. erythropus*, and projects from the head less prominently, but resembles it in other ways sufficiently closely to call for no detailed description. The most important difference is the absence of the tragal thickening in front of the intertragal notch, so that the orifice of the ear is exposed. Owing to the reduction in size of the upper free portion, the supratragus is nearer to the summit and the latter is somewhat more pointed. (Text-fig. 43, E.)

The ear of *Geosciurus capensis* exhibits the final stage in degeneration in this group * ; but it is clearly derivable from the type seen in *Atlantoxerus* by the reduction of the upper portion above the supratragus to a rounded thickened rim incapable of being folded downwards and backwards to any appreciable extent on to the supratragus, which is represented at most by a short ridge running forwards and upwards from the antitragus. The latter, as in the other species, is a rounded thickened bulge, less well defined than in the northern species, set high up and overlapping the posterior portion of the cavity. The anterior rim is overfolded, and its inferior continuation into the cavity is represented at most by a small excrescence opposite the antitragus. There is no tragus, as in *Atlantoxerus*, the orifice being exposed at the bottom of the deep intertragal notch. The ear is closed by the forward movement of the thicker posterior border of the cavity against the anterior, there being no folding of the antitragus or upper rim. (Text-fig. 43, F.)

The structure of the ears in these Bristly Ground Squirrels is not opposed to the view of their affinity with the African species referred to *Funisciurus*, but the differences supply no evidence of close affinity.

In *Castor* the ear is relatively small, but is as free from the integument of the head as in the typical Sciuridæ. Its outer surface is flat, and the anterior edge is not overfolded ; it is uniformly covered with hair except round the cavity, where it is naked. The cavity is a small, irregularly triangular space bounded above by the supratragus, which is overlapped in front by the anterior edge which runs downwards and backwards to the orifice lying at the bottom of the cavity and concealed by the lower edge of the cavity corresponding to the intertragal notch. The posterior border of the cavity forms a convex bulge probably representing the antitragus, but there is no trace of tragus. (Text-fig. 40, C.)

The characters of the principal types of ears above described may be summarised as follows :—

a. Ear simple, its anterior edge above the supratragus not overfolded .... *Castor*.

a′. Ear simple or complex, its anterior edge above the supratragus overfolded.

  b. Cavity of the ear, when folded, mainly closed by hairy, thickened continuation of the overturned anterior rim beneath the supratragus, no tragus or antitragus ... *Citellus*, *Cynomys*, *Marmota*.

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* Described by W. L. Sclater as follows :—Ear conch completely absent, the ear-opening being a narrow diagonal slit half an inch in length.

b′. Cavity of the ear, when folded, mainly closed by antitragus, the inferior continuation of the overfolded anterior border not forming a hairy thickening within the cavity.
  c. Antitragal thickening set high up near the middle of the posterior wall of the cavity; pinna reduced.
    d. Margin of ear a thickened rim not standing away from the head .... *Geosciurus.*
    d′. Margin of ear standing away from head dorsally ... *Xerus*, *Euxerus*, *Atlantoxerus.*
  c′. Antitragal thickening occupying normal position and forming the postero-inferior wall of the cavity; pinna standing well away from head dorsally .... Typical Squirrels, *Tamias*, Petauristidæ.

Although *Castor* is isolated at the head of this table, it can hardly be claimed that its ears differ more from those of typical Squirrels than do the ears of *Geosciurus.* Section c′ is roughly divisible into two groups, exemplified respectively by *Sciurus* and its near allies, *Tamias* and the Petauristidæ, which have long or comparatively long ears, and by the tropical African and Asiatic genera *Funisciurus*, *Heliosciurus*, *Callosciurus*, and *Ratufa*, where the ears are shorter and less tubular at the base. But these groups seem to intergrade. What the ears of *Rheithrosciurus* are like apart from length has yet to be ascertained.

The Feet.

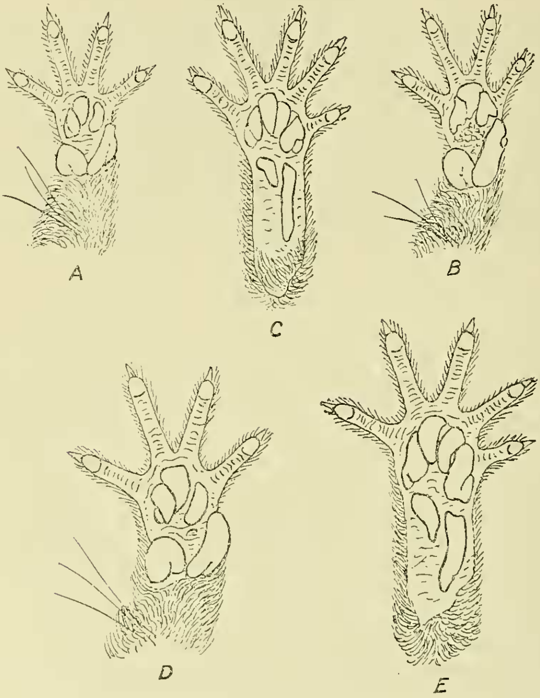
The feet of the typical arboreal Squirrels of the family Sciuridæ have many characters in common. In the fore foot the first digit is reduced to an apparently functionless excrescence springing from or imbedded in the side of the inner carpal pad, and carrying a nail. Of the remaining digits, the fourth is the longest, the difference between the fourth and the fifth or second being considerable. The fourth and the third are more closely united at the base than they are to the fifth or second respectively, and the middle line of the artiodactyle foot passes between them. The digital pads and claws are well developed. The plantar pad is always represented by three well-defined elements. The undersides of the digits and of the sole are typically naked —hairy in some northern forms in winter,—and there are two well-developed carpal pads, of which the inner is the larger of the two. The tuft of carpal vibrissæ is always present and large.

The digits of the hind foot resemble those of the fore foot tolerably closely in structure and relative lengths, the fourth being the longest; but the first digit is well developed and resembles the others, except that it is much the shortest of the series. The well-developed plantar pad consists of four lobes. The metatarsal area is for the most part naked, the heel alone generally being hairy, and is supplied with two pads, an inner, which is the larger, and an outer, which, in addition to being smaller, is set more forwards. Sometimes one or both of these pads is suppressed, in the case, for instance, of Squirrels, which have hairy feet in the winter, e.g. *S. vulgaris*.

a. Feet of the Tropical Asiatic Squirrels.

In *Callosciurus prevosti* the claws of the fore foot are short, with an abruptly curved, sharp point; the three main elements of the plantar pad are large and elongated, and small accessory tubercular pads are sometimes associated with them. The outer carpal pad is irregularly cordate, with a notch in its posterior border; it is much shorter than the inner carpal pad, which extends forwards along the side of the foot, so that its anterior end overlaps on the pollical side the posterior end of the internal lobe of the plantar pad, and its pollical margin, evenly convex, conceals from view from the lower side the nail of the pollex, which is planted some distance behind the anterior end of the pad. (Text-fig. 45, D.)

Text-figure 45.



A. Right fore foot of *Callosciurus notatus*, nat. size.
B. ,, ,, ,, ,, *Tomeutes vittatus.*
C. ,, hind ,, ,, ,, ,,
D. ,, fore ,, ,, *Callosciurus prevosti.*
E. ,, hind ,, ,, ,, ,,

The hind foot has claws like those of the fore foot, and the four lobes of the plantar pad are similarly large and long, especially the internal; and both the internal and the external lobes are provided with a small supplementary lobe, making the entire plantar pad appear to be composed of six lobes, four large and two small. The metatarsal pads are also large. The internal starting close behind the corresponding lobe of the plantar pad and extending backwards to within a short distance of the hairy heel, occupies about one-third of the naked metatarsal area. The external metatarsal pad, about equal in area to the median lobe of the plantar pad, extends obliquely inwards and backwards from a point close behind the plantar pad, its posterior end overlapping the anterior end of the internal metatarsal pad. (Text-fig. 45, E.)

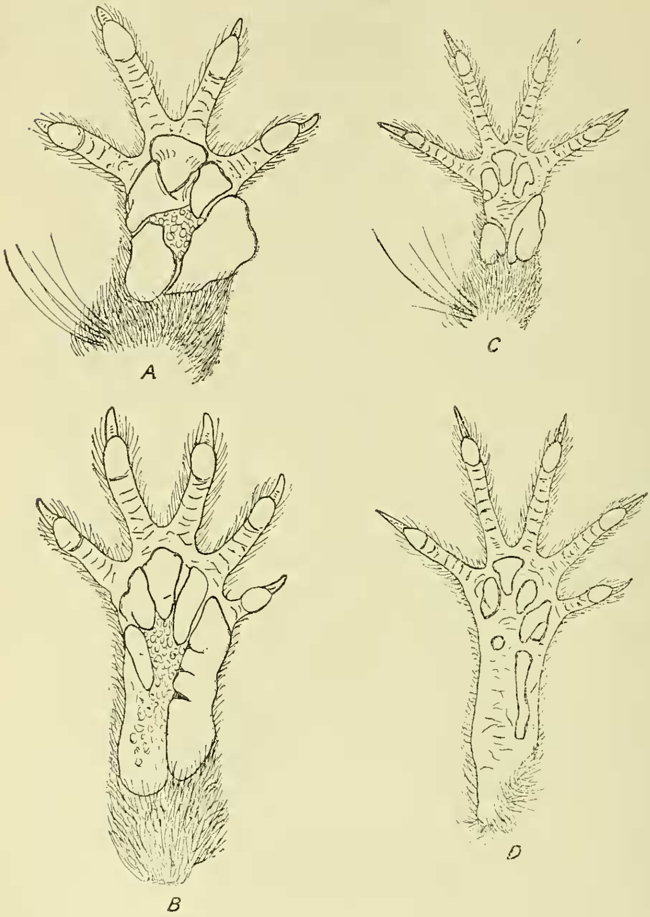
The feet of *Callosciurus notatus* and of *Tomeutes vittatus* are practically alike and agree in all essential respects with those of *C. prevosti*, and judging from dried skins *Callosciurus finlaysoni*, *C. castaneoventris*, and *Tomeutes hippurus* have feet of essentially the same type. (Text-fig. 45, A, B, C.)

In *Ratufa indica* the fore foot has the pads exceedingly large. The three plantar pads are in contact with each other and with the two carpal pads. The latter meet posteriorly, and the five pads form a continuous lobate cushion surrounding a depressed area of soft but coarsely granular integument. The inner carpal, with which the digital pad of the pollex is indistinguishably fused, is as large as the three lobes of the plantar pad taken together. It forms a large projection on the inner side of the foot behind the second digit, and constitutes a grasping organ with the tips of the four digits, which close obliquely upon it. (Text-fig. 46, A.) In the hind foot development of the pads reaches its maximum, as is the case in the fore foot. The four lobes of the plantar pad are wide, long, and in contact, and form a continuous cushion, with undulating distal margin extending from the inner to the outer edge of the foot. The outer metatarsal pad, moreover, is elongated and in contact at its distal end with the outer lobe of the plantar pad; and the inner metatarsal pad is similarly confluent with the inner lobe of the plantar pad, the two together forming a long cushion about half the width of the metatarsal area, and reaching back to the hairy heel. The soft integument of the sole surrounded by the plantar and metatarsal pads and the outer half of the sole as far back as the proximal end of the inner metatarsal pad is granular, the granules being coarser distally behind the plantar pad than proximally towards the heel, which is covered with hair up to the proximal end of the inner metatarsal pad. (Text-fig. 46, B.)

R. bicolor and *R. macrourus* have feet like those of *R. indica*, and the claws of the genus *Ratufa* are short, abruptly curved, and sharply pointed like those of *Callosciurus*. The feet of *Ratufa*, indeed, may almost be described as an exaggeration of the type seen in *Callosciurus* by the expansion and fusion of the pads.

The feet of the Palm Squirrels (*Funambulus*) are relatively longer and thinner than those of *Ratufa* and *Callosciurus*, and have the pads less well developed. Otherwise they are tolerably similar to those of *Callosciurus*, the inner, or pollical, carpal pad being similarly elongated, so that its distal extremity considerably overlaps the inner lobe of the plantar pad. In the hind

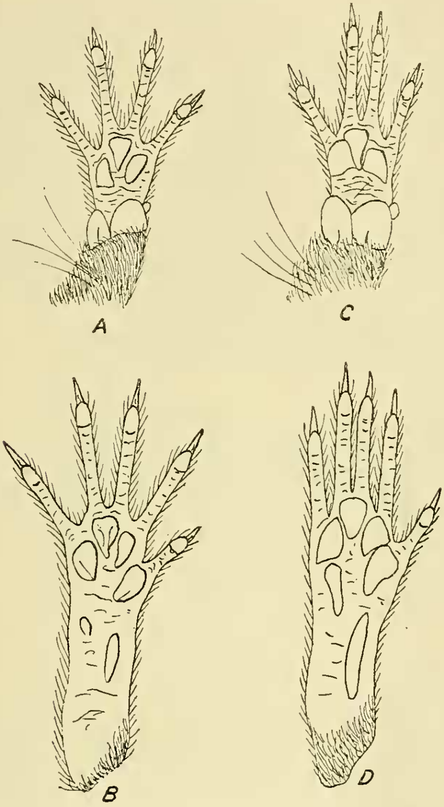
Text-figure 46.



A. Right fore foot of *Ratufa indica*. × $\frac{1}{3}$.
B. „ hind „ „ „ „
C. „ fore „ „ *Funambulus palmarum*, much enlarged.
D. „ hind „ „ „ „

foot the external and internal lobes of the plantar pad are often subdivided, but not always, and never to the same extent as in *Callosciurus*; the inner metatarsal pad is always long and rod-like, but the outer in all the specimens examined is small, spherical, and approximately on a level with the distal end of the inner without overlapping it proximally. The heel is less hairy than in *Callosciurus* and *Ratufa*, being sometimes naked in the middle line, sometimes scantily hairy. (Text-fig. 46, C, D.)

Text-figure 47.



A. Right fore foot of *Rheithrosciurus macrotis.*
B. ,, hind ,, ,, ,, ,,
C. ,, fore ,, ,, *Protoxerus stangeri.*
D. ,, hind ,, ,, ,, ,,

(These figures drawn without measurements from dried skins.)

Judging from dried skins*, the feet of *Rheithrosciurus* are relatively longer and thinner than those of *Callosciurus*, and the claws are longer. In the fore foot the three plantar lobes are large, the median being well defined from the laterals. Of the carpal pads, the outer is the smaller and narrow, and the inner has an evenly convex margin and is not elongated and produced distally so as to overlap the plantar lobe of the same side. In the hind foot the four lobes of the plantar pad are not so large or so closely packed as in *Callosciurus*, and the outer and inner are at most indistinctly subdivided; the metatarsal area is naked to the heel, the outer metatarsal is considerably shorter than in other Oriental genera examined, and the inner metatarsal is small and subspherical as in *Funambulus* and many other genera of Squirrels. (Text-fig. 47, A, B.)

In the structure of the feet *Rheithrosciurus* is perhaps more like some of the American subgenera of *Sciurus* than it is like other Oriental genera.

The distinguishing characters of the feet of the Oriental Squirrels above described may be tabulated as follows:—

- *a*. Pads enormous, internal carpal very prominent on the pollical side; metatarsal pads confluent with plantar pad, the internal nearly half the width of the metatarsus …… *Ratufa*.
- *a′*. Pads less developed, internal carpal less or not noticeably prominent on pollical side; metatarsals not confluent with plantar pad.
  - *b*. Internal carpal long, narrowed distally, and overlapping plantar pad on inner side; internal metatarsal long.
    - *c*. Feet shorter and stouter, plantar pad of hind foot larger, six-lobed, metatarsals thicker, external produced proximally beyond distal end of internal. *Callosciurus*, *Tomeutes*.
    - *c′*. Feet longer and thinner, pads smaller; external metatarsal spherical set beyond distal end of narrowed internal metatarsal…………………………………… *Funambulus*.
  - *b′* Internal carpal pad apically rounded, only a little longer than external and not reaching plantar pad; internal metatarsal relatively short…………………………………… *Rheithrosciurus*.

b. Feet of the Tropical African Squirrels.

The two African species, *Funisciurus leucostigma* and *F. cepapi*, have feet of a more generalised type than those of the Oriental species of *Ratufa* and *Callosciurus* examined, the plantar, carpal, and metatarsal pads being less well developed. The plantar pad of the fore foot is three-lobed, of the hind foot four-lobed. The inner carpal pad is not so elongated distally, and the outer metatarsal is comparatively small, subcircular, or elliptical, and is set on a level with the anterior end of the long rod-like inner metatarsal or a little in front of it. Except that the feet are of stouter build, they differ but little from those of *Funambulus palmarum*, although in the latter the inner carpal pad is produced distally nearly as much as in *Callosciurus*. (Text-fig. 48, C–F.)

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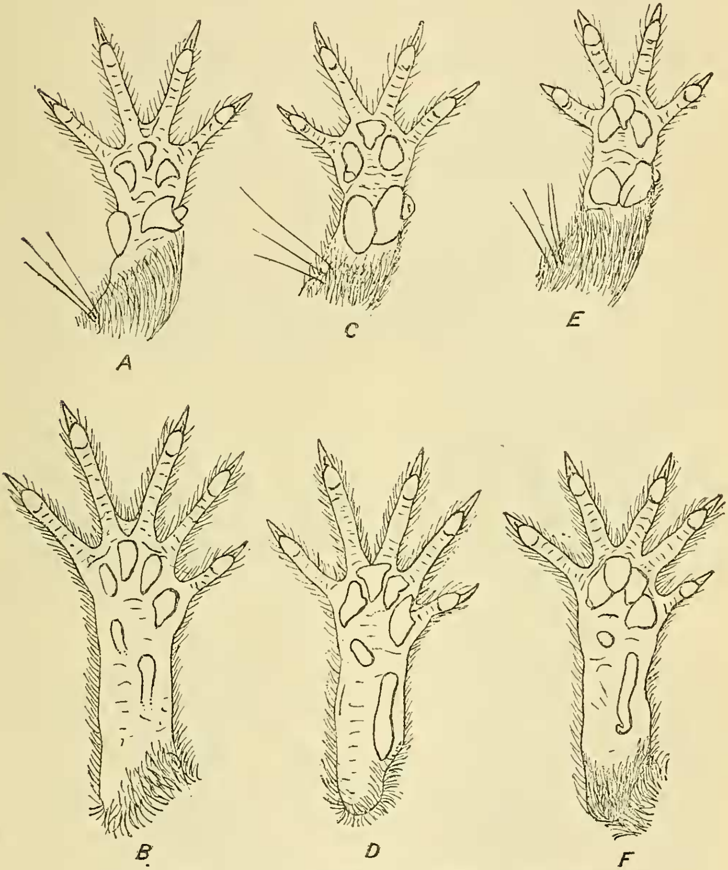
* It must be remembered, however, that the proportions of the feet vary with the preservation. In fresh specimens they appear to be plumper and shorter than those contracted by alcohol, and the latter are, as a rule, less shrunk than the feet on dried skins.

Judging from dried skins, the feet of *F. isabella*, the type of the genus *Funisciurus*, resemble those of *F. leucostigma* and *cepapi*.

Protoxerus stangeri also has feet differing in no important point from those of *Funisciurus*, although the outer metatarsal pad is much longer, being at least half as long as the inner. (Text-fig. 47, C, D.)

Text-figure 48.



A. Right fore foot of *Heliosciurus punctatus*, nat. size.
B. ,, hind ,, ,, ,, ,, ,, ,,
C. ,, fore ,, ,, *Funisciurus cepapi*, ,, ,,
D. ,, hind ,, ,, ,, ,, ,, ,,
E. ,, fore ,, ,, *Funisciurus leucostigma*, ,, ,,
F. ,, hind ,, ,, ,, ,, ,, ,,

In *Heliosciurus punctatus* the feet are relatively larger than in *Funisciurus leucostigma*, the plantar lobes and carpal pads of the fore foot are smaller, more angular, and separated; in the hind foot the plantar lobes are also smaller and more spaced, the inner metatarsal is much shorter, being oval and well-defined distally but abbreviated and ill-defined proximally; the inner metatarsal is like it but smaller [*]. (Text-fig. 48, A, B.)

The species belonging to the three African genera above discussed may be distinguished as follows by their feet:—

a. Inner metatarsal pad very short, lobes of plantar pads and carpal pads relatively small and separated .... *H. punctatus.*
a′. Inner metatarsal pad a long, stout ridge; lobes of plantar pads and carpal pads larger and closer together.
  a^2. Outer metatarsal pad elongate, more than half the length of the inner .... *P. stangeri.*
  b^2. Outer metatarsal pad small, oval or spherical ...... *F. leucostigma, cepapi.*

In a general sense the hind feet of *Funisciurus* do not differ in any very important respect from those of *Funambulus*; but all the African species examined differ from all the Oriental species in not having the same elongation of the inner carpal pad. In the length of the outer metatarsal *P. stangeri* approaches *Ratufa* and *Callosciurus*.

Funisciurus leucostigma and *cepapi*, on the one hand, and *Protoxerus stangeri*, on the other, were regarded by Forsyth Major as representing respectively two subgenera of *Xerus*. By their feet, however, they are typical arboreal Squirrels, differing in no essential particulars, so far as those organs are concerned, from such tropical American species as *Sciurus* (*Echinosciurus*) *hypopyrrhus*.

c. *Feet of the European and American Squirrels.*

In the tropical American Squirrels, referred to a large number of subgenera of *Sciurus*, the soles of the feet are naked as in the tropical Asiatic and African forms, the heel being generally hairy although sometimes naked down the middle line, as in an example of *Sciurus saltuensis bondæ* that died early in October. The lobes of the plantar pads are well developed, the two carpal pads are subequal in size, the inner not projecting appreciably beyond the outer as it does in the tropical Asiatic forms. The two metatarsal pads are retained, the inner being thick, elongated, and curved, the outer smaller, ovate, and situated in front of the anterior end of the inner. The claws are longer than in the tropical African and Asiatic forms. The feet of *S.* (*Echinosciurus*) *hypopyrrhus* resemble those described above, and their soles are naked in mid-winter. (Text-fig. 49, D.)

The feet of the Squirrels of the northern parts of America are, generally speaking, similar to those of the warmer latitudes, with this difference, that the soles undergo a seasonal change in the matter of hair growth, accompanied in some cases by the suppression of one or both of the metatarsal pads.

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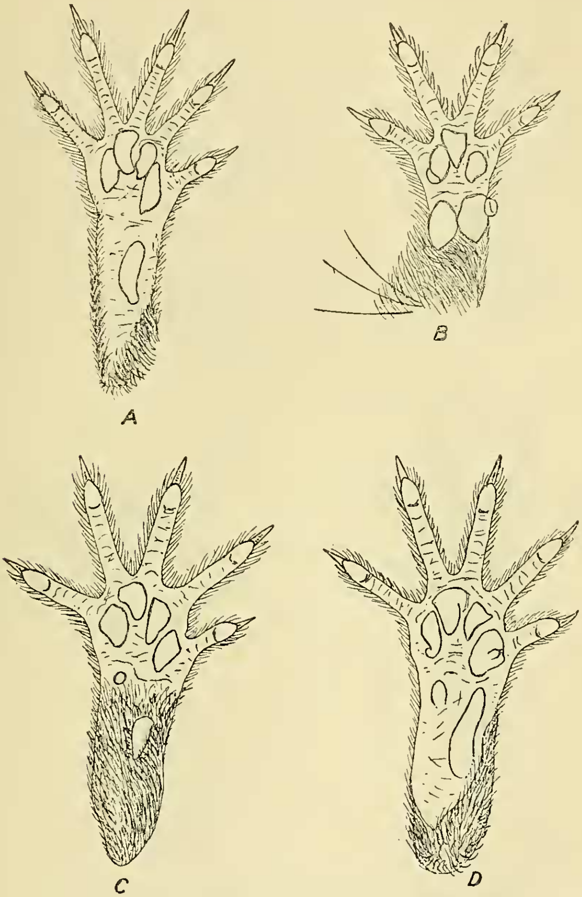
[*] For a tabulation of the genera of African Sciuridæ, based mainly on skulls and teeth, see Thomas's paper (Ann. & Mag. Nat. Hist. (8) iii. pp. 467–475, 1909).

In the North American Grey Squirrel (*S.* (*Neosciurus*) *carolinensis*) the outer metatarsal pad is sometimes absent. When retained it is a hemispherical tubercle set far forwards in front of the inner, which is irregularly ovate and shorter than in

Text-figure 49.



A. Right hind foot of *Sciurus carolinensis*, with external metatarsal pad absent, in summer pelage (from dried skin).

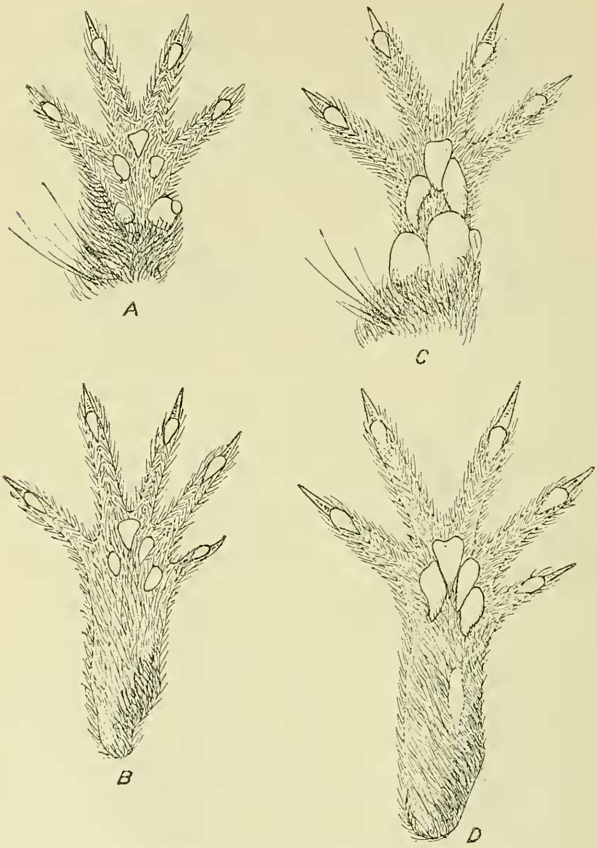
B. Right fore foot of the same, in winter pelage.

C. „ hind foot of the same, in winter pelage, the external metatarsal retained.

D. Right hind foot of *S. hypopyrrhus*, or closely related species, in midwinter pelage.

the tropical species. An example examined in September had the sole of the hind foot naked except the heel, which was hairy, whereas one that died in the middle of December had the sole covered with hair as far down as the outer metatarsal pad.

Text-figure 50.



A. Right fore foot of *Sciurus vulgaris*, mid-winter.
B. ,, hind ,, ,, ,, ,, ,, ,,
C. ,, fore ,, ,, *S. niger rufiventer*, ,, ,,
D. ,, hind ,, ,, ,, ,,
(C, D from dried skin.)

The fore foot in the two specimens was quite naked beneath at both dates. Again, in a skin of a specimen of the North American Fox Squirrel *S.* (*Parasciurus*) *niger rufiventer*, which died at the beginning of December, all trace of the outer metatarsal pad has disappeared, although the inner is somewhat larger and more elongated than in *S. carolinensis*, and the whole of the under side of the foot, including the digits, is covered thickly with hair, apart from this pad, the well-developed four-lobed plantar pad, and the digital pads. The latter are pointed at their proximal ends. The fore foot is similarly hairy, there being a distinct patch on the median area in front of the carpal pads and defined by the three elongated contiguous lobes of the plantar pad. I am not aware whether the soles of the feet in this species are naked in the summer or not; but analogy justifies the belief in this being so. (Text-figs. 49, A–C; 50, C, D.)

In *Sciurus vulgaris* * and its subspecies the lower sides of the feet in summer are as naked as in tropical species, except that perhaps a larger area of the heel is hairy. The inner metatarsal pad is comparatively short and set some distance behind the plantar pad; the outer is quite small and some distance in front of the anterior end of the inner. But in winter the soles and lower sides of the digits are overgrown with hair which is more abundant on the hind than the front foot. In the hind foot it obliterates the metatarsal pads and passes between the lobes of the plantar pads. In both feet at this season the digital pads are reduced to long, narrow, posteriorly-pointed lobes. (Text-fig. 50, A, B.)

In the North American Red Squirrel, *S.* (*Tamiasciurus*) *hudsonicus*, I can find no trace of either of the metatarsal pads. According to C. B. Cory † the soles of the feet are "furred in the winter." From this statement I should infer that they are naked in the summer, were it not that a skin in the Zoological Society's collection in summer pelage, with untufted ears and black lateral stripe, has the metatarsus covered with hair almost down to the plantar pads, whereas the area round the plantar pads and the under sides of the digits are naked. The fore foot also is as naked as in tropical species of Squirrels. On the other hand, in the skin of a specimen that died on January 7th in winter pelage, with tufted ears and no lateral stripe, both fore and hind feet are covered with hairs beneath, as in the specimen of the Fox Squirrel described, only the digital, plantar, and carpal pads being naked. But whether the whole of the metatarsal area in the American Red Squirrel is mesially naked back to the heel in summer as in the European Squirrel, *S. vulgaris*, I do not know. (Text-fig. 51, A, B.)

d. Feet of the Chipping Squirrels (Tamias).

The feet of the Chipmunk, *Eutamias quadrivittatus*, do not differ materially from those of the typical Squirrels, except that the third and fourth digits are very nearly equal, the fourth at most exceeding the third very slightly. Nevertheless, the tip of the fourth extends beyond that of the second both in the fore and the hind foot. The feet are narrow and long, and the lobes of the plantar pads are not in contact, though well developed. The inner lobe of the carpal pad has a rounded distal border and is not produced beyond the margin of the smaller outer pad, and the small pollex projects a little in front of it, which is not the case in the typical Squirrels, where the pollex rises from the outer surface of the inner carpal. The under sides of the digits and the area round the plantar lobes are naked in both fore and hind foot; but in the hind foot the whole of the meta-

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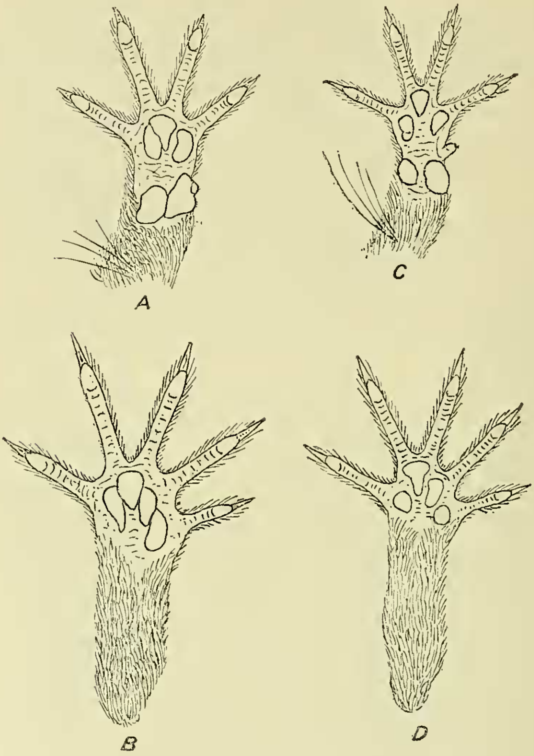
* The feet, in summer and winter pelage, of the British representative (*S. leucourus*) of the species are figured and described by Barrett-Hamilton and Hinton ('A History of British Mammals,' pt. xxi. p. 699, pl. xxxvii.).

† 'The Mammals of Illinois and Wisconsin,' 1912, p. 123.

Text-figure 51.



A. Right fore foot of *S. hudsonicus*, in summer pelage (from dried skin).
B. „ hind „ „ same specimen.
C. „ fore „ „ *Eutamias quadrivittatus.*
D. „ hind „ „ „ „

(A, B a little enlarged; C, D much enlarged.)

tarsal area is covered with hair down to the plantar pad, and there is no trace of metatarsal pads as in *S.* (*Tamiasciurus*) *hudsonicus.* (Text-fig. 51, C, D.)

This description of the feet of *Eutamias*, based upon a single individual, must not be taken as applying to all the species of *Tamias.* In some dried skins of this genus in the Natural History Museum, the digits appear to resemble those of *Citellus* rather than of *Sciurus* and its allies in relative lengths; and the metatarsal area is not so extensively haired as in the specimen of *Eutamias* described.

e. Feet of the Bristly Ground Squirrels (Xerus, *etc.*).

The feet of the African Ground Squirrels, *Atlantoxerus getulus*, *Xerus rutilus*, *Euxerus erythropus*, and *Geosciurus capensis* differ from those of the arboreal species hitherto described in having the third digit the longest and the fourth only a little longer than the second, so that the feet approach the perissodactyle type; the pollex is not suppressed to quite the same extent, but stands away as a distinct excrescence from the antero-external edge of the adjoining inner carpal pad, and this is not appreciably produced distally beyond the outer carpal; the metatarsal area is naked to the heel, and its pads are either absent or poorly developed.

In *Atlantoxerus getulus* the feet are long and slender and the digits more nearly approach those of the arboreal Squirrels in length, the third only slightly exceeding the fourth, which, in the fore foot, is decidedly longer than the second. The lobes of the plantar pads are large, well developed, the hallucal lobe on the hind foot being nearly as large as the others individually; the carpal pads also are comparatively large, and the metatarsal pads are at all events sometimes distinguishable, although small and oval. (Text-fig. 52, A, B.)

In *Euxerus erythropus* the fore foot is broader and shorter, with respect both to the digits and sole, than in *Atlantoxerus*; the plantar and carpal pads are relatively smaller and the claws are longer. The pollex is small but subcylindrical with a small pad remote from the carpal. In the hind foot, too, the claws are longer than in *Atlantoxerus*, the lobes of the plantar pad are considerably smaller, especially the outer and inner, the latter being a small subcircular tubercle at the base of the hallux, only about one-fourth the size of the median lobe: and there is no trace of metatarsal pads*. (Text-fig. 53, A, B.)

In *Geosciurus capensis* the feet are more robust and more fossorial in character than in *E. erythropus.* In the fore foot the three lobes of the plantar pad are well developed but shorter than in *Atlantoxerus* and in contact, and the pad of the pollex projects as a large lobe jutting out from the side of the adjoining carpal pad. In the hind foot the three main lobes of the plantar pad are also well developed, larger than in *Euxerus erythropus* but shorter than in *Atlantoxerus getulus*; but the hallucal lobe is quite small, subcircular and isolated as in *Euxerus erythropus*; and as in the latter there is no trace of metatarsal pads, and the claws of all the digits are long and strong.

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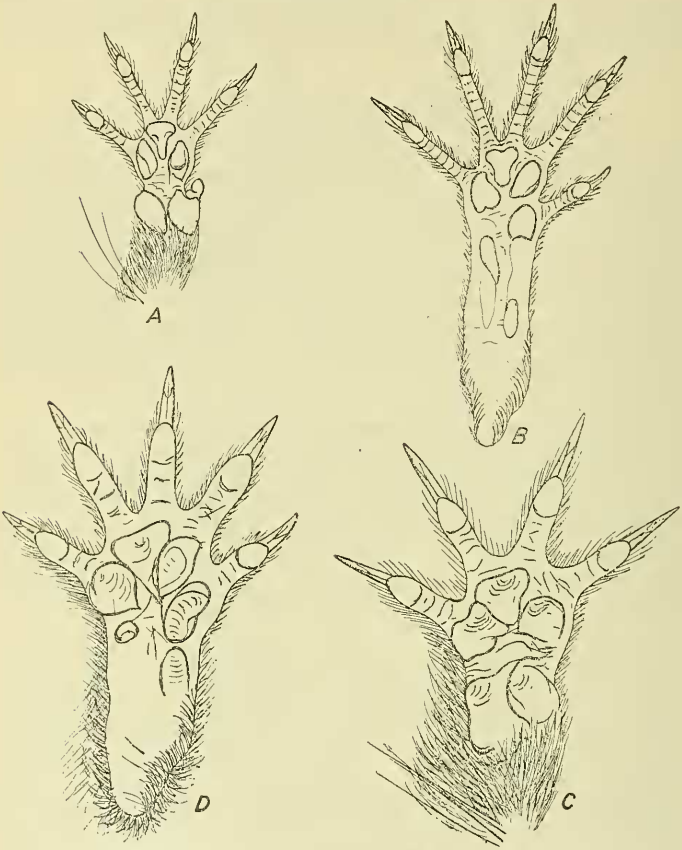
* *X. rutilus* is known to me only from a dried skin. On this the plantar lobes appear to be somewhat larger relatively than in *E. erythropus*; but there is no trace of metatarsal pads, and the hallucal lobe of the plantar pad is small and isolated.

Text-figure 52.



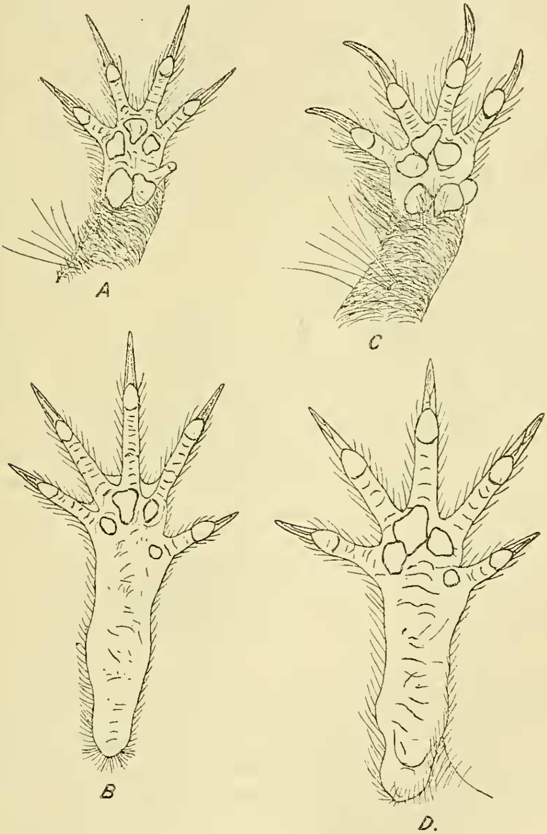
A. Right fore foot of *Atlantoxerus getulus*, much enlarged.
B. „ hind „ „ same.
C. „ fore „ „ *Marmota marmota*. × ⅓.
D. „ hind „ „ same.

The feet of the Xerine Squirrels above described differ as follows:—

a. Feet thinner; inner lobe of plantar pad of hind foot large, the metatarsal pads retained but poorly defined .... *Atlantoxerus.*
a′. Feet stouter; inner lobe of plantar pad of hind foot very small, metatarsal pads absent.
  b. Plantar pads smaller, pollex a relatively small subcylindrical excrescence .... *Euxerus.*
  b′. Plantar pads larger, pollex a conspicuous subcircular excrescence .... *Geosciurus.*

The feet of *Xerus*, typified by *rutilus*, fall under heading *a′* of this table.

Text-figure 53.



A. Right fore foot of *Euxerus erythropus*. × ¼.
B. ,, hind ,, ,, ,, ,,
C. ,, fore ,, ,. *Geosciurus capensis*.
D. ., hind ,, .,, ,, ,,

f. Feet of the Sousliks and Marmots.

A second group of Ground Squirrels represented by the Sousliks (*Citellus*) and the Marmots (*Cynomys*, *Marmota*) have feet like those of *Xerus* and its allies in that the third digit is the longest, and the second and fourth digits not so unequal, as in the arboreal Squirrels, and the claws longer, stouter, and less curved. The three genera in question, however, have very different feet.

The fore foot of *Citellus* (*Otospermophilus*) *beecheyi*[*], judging from a dried skin, is shorter and broader than that of the typical squirrels, and is naked below. The fourth digit is decidedly but not much longer than the second. The three lobes of the plantar pad and the two carpal pads are well developed, and the pollex is represented by a conspicuous nail attached to the outer side of the inner carpal pad in front. In the hind foot the second, third, and fourth digits are nearly equal, the third only slightly surpassing the others, which are subequal; the fifth reaches beyond the middle of the fourth; the plantar pad is represented by four well-developed contiguous lobes, the inner and outer of which are set rather far back, the greater part of each lying behind the other two. There is no trace of metatarsal pads, the whole area being covered with hair from the heel to the plantar pad. (Text-fig. 54, A, C.)

Judging from Miller's description of the European species *Citellus citellus*, the feet of that species agree tolerably closely with those of *C. beecheyi*. He says, however, that in the fore foot the second and fourth digits are subequal, and that the fifth extends only a little beyond the base of the fourth. This does not apply to *C. beecheyi*. Similarly, he states that in the hind foot of *C. citellus* the fifth digit extends just beyond the base of the fourth, and the hallux not quite to the base of the second digit. This is not true of *C. beecheyi*. But the apparent differences between the two species in the particulars mentioned are interesting, if true, because in the relative length of the digits the typical European species seems to approach the genus *Cynomys*[†].

In *Cynomys* the fore foot is long and robust, almost as large indeed as the hind foot. The digits are thick and the claws long. The second digit is a little longer than the fourth, and the fifth reaches a little beyond the base of the fourth. The inner and outer lobes of the plantar pad are small, and together hardly equal the size of the wide median lobe. The outer carpal pad is large and the inner is rather prominent internally, and gives support to the claw of the pollex, which is as long as that of the second digit. The entire sole is naked. In the hind foot the second, third, and fourth digits are subequal, the third only very slightly surpassing the others, as in *Citellus*. The fifth is set almost as far back as the hallux and is only a little longer, surpassing by a little the base of the fourth. The claws on these digits are shorter than on those of the fore foot. There are four well-developed separated lobes constituting the plantar pad, and their arrangement is quadrate, the outer and inner lying behind the others—an arrangement foreshadowed in *Citellus*. There are no metatarsal pads, the sole being naked except for a band of hair passing from the inner side of the heel forwards along the

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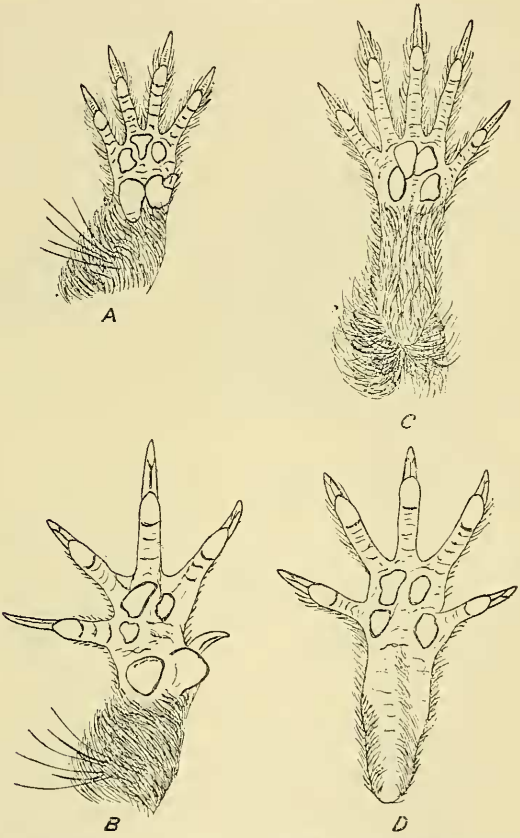
[*] A Californian species.

[†] For a possible explanation of these discrepancies, see note, p. 1208.

Text-figure 54.



A. Right fore foot of *Citellus* (*Otospermophilus*) *beecheyi*, from dried skin.
B. „ „ „ „ *Cynomys ludovicianus*. × $\frac{1}{4}$.
C. „ hind „ „ *Citellus* (*Otospermophilus*) *beecheyi*, from dried skin.
D. „ „ „ „ *Cynomys ludovicianus*. × $\frac{1}{4}$.

middle of the metatarsal surface nearly or quite up to the level of the hallucal lobe. (Text-fig. 54, B, D.)

The feet of *Marmota marmota* are relatively more robust and somewhat shorter in the digits than those of *Cynomys*. In the fore foot the three lobes of the plantar pad are relatively larger, occupying practically the entire width of the foot. The carpal pads also are larger, but the inner does not project laterally in the same way and has no trace of the pollex. Similarly, in the hind foot the plantar lobes are massive and do not exhibit that quadrate arrangement seen in *Cynomys* and *Citellus*. Behind the outer lobe of the plantar pad there is a hemispherical external metatarsal, and behind the inner plantar a short internal metatarsal with ill-defined posterior border. (Text-fig. 52, C, D.)

A peculiarity of the feet of this species of *Marmota* is the complete absence of the pollex. Miller noted this in twenty skins, Tullberg's figure showed the same thing, and I have not succeeded in finding a trace of this digit in some half-a-dozen examples I have seen. On the other hand, Miller records the presence of the pollex with a flattened nail in *M. bobak*, the other European species. The presence of a rudimentary thumb is cited by Blanford in his generic diagnosis of *M. himalayana*, *hodgsoni*, and *caudata*, and American writers testify to its retention in *M. monax* and other N. American species.

By the structure of the feet the Marmotine genera may be arranged as follows:—

a. Feet very powerful; lobes of plantar pads and carpal pads large, metatarsal pads retained.
  b. Pollex suppressed.......... *Marmota*.
  b'. Pollex retained.......... *Marmotops** nov.
a'. Feet at most moderately powerful; lobes of plantar pads and carpal pads smaller, no metatarsal pads.
  c. Feet comparatively stout, inner carpal pad projecting, a long claw on pollex.......... *Cynomys*.
  c'. Feet comparatively slender; inner carpal pad normal; pollex with nail.......... *Citellus*.

g. Feet of the Flying Squirrels (Petauristidæ).

Apart from the cartilaginous rod supporting the patagium and jointed to the wrist just behind the outer carpal pad, the fore feet of the Petauristidæ closely resemble those of the typical arboreal squirrels. In *Petaurista albiventer* (*magnificus*)† the claws are long and strongly curved. The digits also are long and markedly unequal in length, the fourth being considerably longer than the third and fifth, which are subequal and surpass the second. On the specimen examined there is practically no external trace of pollex and none of the nail. The three lobes of the plantar pad and the carpal pads are large and striate all over. (Text-fig. 55, A.)

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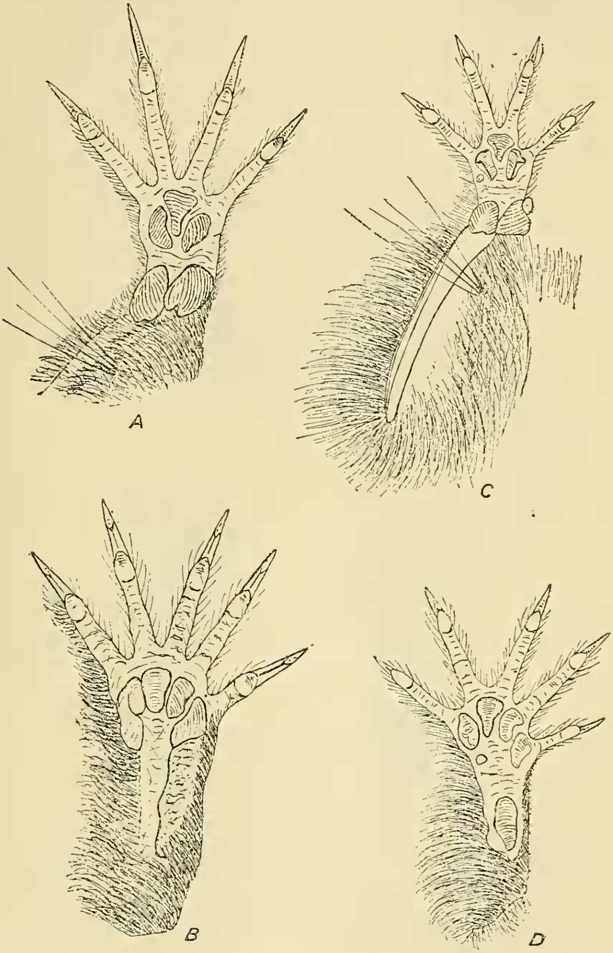
* Type, *M. monax*.

† For the specific names here used for *Petaurista* (*olim Pteromys*), see Wroughton, Journ. Bombay Nat. Hist. Soc. xx. p. 1012, 1911.

On the hind foot the claws are similar, but the digits are shorter, the second, third, fourth, and fifth appearing to be nearly equal, although in reality the fourth is a little longer than the third, which is about equal to the fifth and slightly longer than

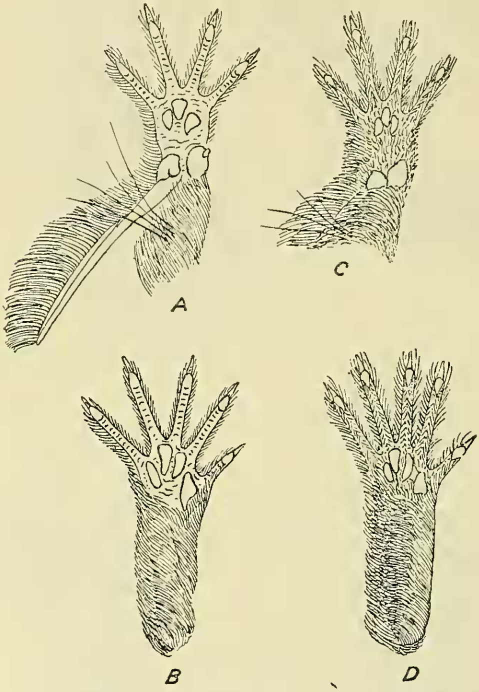
Text-figure 55.



A. Right fore foot of *Petaurista albiventer,* from dried skin.
B. „ hind „ „ „ „ „ „ „
C. „ fore „ „ *Eoglaucomys fimbriatus,* showing the patagial rod. $\times \frac{1}{4}$.
D. „ hind „ „ same.

the second. The four lobes of the plantar pad are large, the outer and inner being larger than the others. The inner metatarsal pad is well developed, and extends as in *Ratufa* along the inner side of the metatarsal area, being in contact with the plantar pad distally. A large area of the heel is covered with hair, and on the outer side of the foot the hair overgrows the sole up to a line continuous with the proximal extremity of the large, long, outer plantar lobe, so that the area of naked skin on the admedian side of the metatarsal pad is narrow. (Text-fig. 55, B.)

Text-figure 56.



A. Right fore foot of *Glaucomys volans,* summer pelage.
B. ,, hind ,, ,, ,, ,, ,, ,,
C. ,, fore ,, ,, ,, *stramineus,* winter pelage,
D. ,, hind ,, ,, ,, ,. ,, ,,

Blanford described the hind foot of this species, under the name *Pteromys magnificus*, as similar to that of *P. inornatus*, saying of the latter: "The large metatarsal pad joins the inner toe pad. . . . No supplementary pad." This agrees with my observations; but from the size and length of the outer lobe of the plantar pad I suspect the outer metatarsal pad, referred to by Blanford as the supplementary pad, is retained and fused with it. According to Blanford the feet of *P. yunnanensis* are like those of *albiventer* but larger, whereas in *P. philippensis* (*oral*) there is a large piriform inner and a small outer metatarsal pad, and *P. caniceps* seems to resemble *philippensis* so far as the inner pad is concerned, although Blanford makes no mention of the presence of an outer pad.

In *Eoglaucomys fimbriatus* the fore foot does not differ materially from that of *Petaurista albiventer* except that there is a distinct pollical excrescence with a nail, as in the typical Sciuridæ, and the plantar and carpal pads carry coarser ridges not distributed all over them but limited to the highest portion of the pads. In some cases there is a little isolated tubercle on the outer side of the external lobe; in other cases this is confluent with the lobe, increasing its width. The hind foot is also tolerably similar to that of *P. albiventer*; the sculpturing of the pads, however, differs as in the fore foot and the inner metatarsal pad, about twice as long as wide, is set at the proximal end of the naked metatarsal area remote from the hallucal lobe of the plantar pad. In this species also, as noticed by Blanford, there is a small circular outer metatarsal pad behind and close to the outer lobe of the plantar pad. If this were enlarged and confluent with the plantar pad, the outer lobe of the latter would resemble tolerably closely that of *Petaurista albiventer*. (Text-fig. 55, C, D.)

None of the other Indian species assigned by Blanford to *Sciuropterus** retains the outer metatarsal pad. *S.* (*Hylopetes*) *alboniger* has the inner metatarsal pad oval; in *S.* (*Petinomys*) *fuscocapillus* it is very elongate; in *Belomys pearsonii* it is oval.

In the North American species, *Glaucomys volans*, the fore foot structurally resembles tolerably closely that of the Himalayan *Eoglaucomys fimbriatus*. In a spirit specimen of unrecorded date the underside of the digits and of the entire sole of the foot is naked, whereas in a specimen of *G. stramineus*, which died in December, these surfaces are covered with hair, the pads, which appear to be smaller, alone being naked. The hind foot, however, differs in two correlated characters from that of *Eoglaucomys fimbriatus*: there is no trace of metatarsal pads, and the metatarsal area is covered thickly with hair from the heel almost to the plantar pad. In the example of *G. volans*, with the naked sole to the fore foot, the undersides of the digits of the hind foot and the area round the plantar pad are likewise naked, whereas in the specimen of *G. stramineus*, with hairy soled fore foot, the lower sides of the digits and the area round the plantar pad are hairy, like the rest of the sole, and the claws are almost concealed. It is probable that the difference between these two closely-related forms in the matter of the hairiness of the soles of the feet is a seasonal difference comparable to that of *Sciurus vulgaris* and of *S.* (*Tamiasciurus*) *hudsonicus*. (Text-fig. 56.)

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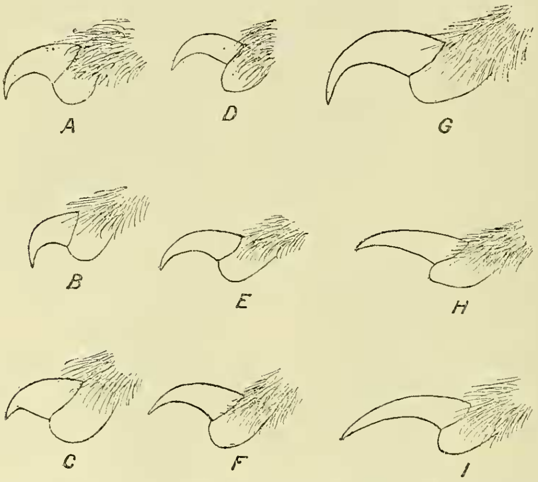
* For the generic and subgeneric names here used for these species, see Thomas, Ann. & Mag. Nat. Hist. (8) i. pp. 1-8, 1908.

Judging from Miller's description, the feet of *S. russicus*, the type of the genus *Sciuropterus*, closely resemble those of the North American species. It might have been taken indeed from the specimen referred to above as *S.* (*G.*) *stramineus*, the soles of the fore foot being thinly haired between the pads, whereas those of the hind foot are covered with a "dense growth of long woolly hairs especially conspicuous along the inner* side, and adding much to apparent width of foot." Miller had only three specimens of this species for examination, and in the absence of information as to the dates of their capture, it is not possible to guess whether there is a seasonal change in the hairiness of the soles of the feet or not.

Text-figure 57.



A. Claw of *Funisciurus leucostigma*; B. *Funisciurus cepapi*; C. *Ratufa indica*; D. *Eutamias quadrivittatus*; E. *Sciurus lindernicus*; F. *Sciurus vulgaris*; G. *Petaurista albiventer*; H. *Citellus beecheyi*; I. *Xerus rutilus*.

To draw attention to the facts here recorded in the hope that they may be amplified and, if necessary, corrected by other workers with more and better material, I subjoin the following table :—

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* For "inner" here read "outer," the error below referred to under *Castor* of confusion between the inner and outer sides of the feet being repeated. The inner side of the foot as generally understood is the side on which the hallux, or first digit, rises, whereas the fringe of hairs on the hind foot of the Petauristidæ is always on the side of the fifth digit, *i. e.*, the outer.

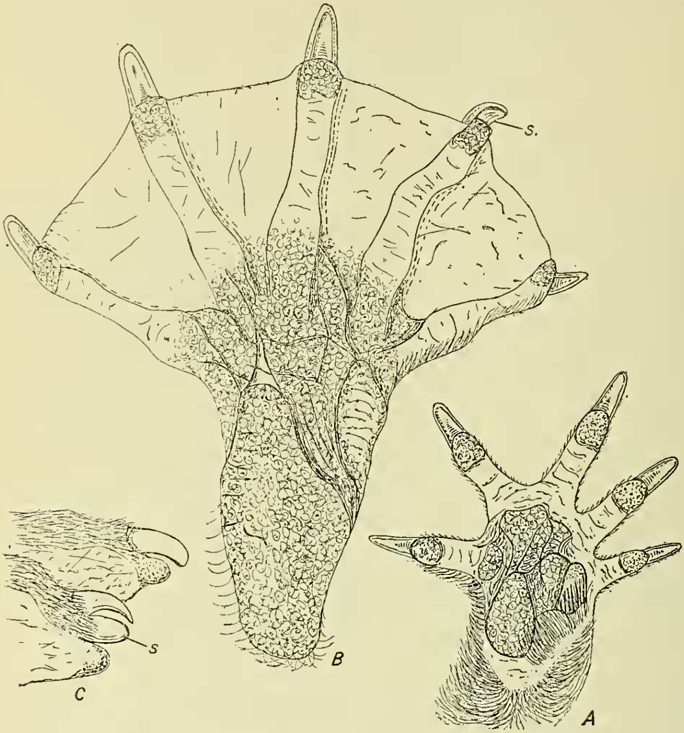
a. Metatarsal area hairy, without pads ……………………	*Sciuropterus*, *Glaucomys*.
a′. Metatarsal area partially naked with the inner pad at least retained.	
b. Inner metatarsal pad confluent with plantar pad; pollex practically suppressed, without nail ……	*Petaurista albiventer*.
b′. Inner metatarsal pad distinct from plantar pad; pollex as in typical Sciuridæ.	
c. Outer metatarsal pad retained ……………………	*Eoglaucomys fimbriatus*.
c′. Outer metatarsal pad lost.	
d. Inner metatarsal pad elongate……………………	*Petinomys fuscocapillus*.
d′. Inner metatarsal pad oval ……………………	*Belomys pearsoni*, *Hylopetes alboniger*.

h. Feet of the Beaver (Castor).

Apart from minor differences, the fore foot of *Castor fiber* differs from that of the Sciuridæ and Petauristidæ in two important points, the presence of a well-developed pollex and the indistinctness of the lobes of the plantar pad. The digits are short, with roughened but not well-defined digital pads; the third is the longest, a little exceeding the fourth, the second and fifth being shorter, and the first, or pollex, the shortest of all. All are armed with long, wide, blunt, slightly curved claws, that of the pollex being a little narrower, sharper, and more curved than the rest. The plantar area is granularly reticulated, and the lobes of the plantar pads are obscurely represented by mobile folds of thickened granular skin, hardly alike in any two specimens or even on the two feet of an individual. Only sometimes are the thickenings arranged so as to indicate the three main plantar lobes present in all the Sciuridæ. Behind the plantar area there are two well-developed elongated carpal pads. The inner at the base of the pollex is the smaller, and is hard, smooth, and grooved except at its distal end. The outer pad is much longer and wider, and extends considerably further up the wrist proximally. The comparatively wide space between these pads is occupied by thickened granular skin, which on the admedian side of the inner carpal pad, and a little in front of it, forms sometimes a lobate thickening, which may represent the inner or pollical element of the plantar pad, which should be present with a well-developed pollex, but which is absent in all the Sciuridæ, where the pollex is little more than a vestigial remnant. There is a rim of naked skin behind these carpal pads; but on the inner side of the wrist the hairs are directed obliquely towards the middle line, in a crest overlapping the posterior portions of the pads. There are no carpal vibrissæ, which are present in all Sciuridæ. (Text-fig. 58, A.)

The hind foot greatly surpasses the fore foot in size, far more so than in any member of the Sciuridæ. This is mainly due to the immense length of the digits, especially of the first and fifth, which, relatively to the other digits, are much longer than in the Squirrels, and give a wide span to the foot. The third and fourth digits are subequal, the fifth is not very much shorter than the fourth and is about equal to the second, and the elongated hallux extends beyond the middle of the second. They are all connected by wide webbing, which extends to the apex of the digital pads or nearly so. These pads are represented by areas of granular skin, and on the first and second digits they form movable lobes, whereas on the third, fourth, and fifth they are less prominent and not separately movable. A well-known peculiarity is the presence of a secondary "false claw" beneath the normal claw of the second digit, constituting with it a fur-

Text-figure 58.



A. Right fore foot of *Castor fiber*. × ½.
B. „ hind „ „ „ „
C. Apex of second and third digits of the same, showing the supplementary claw (*s*) beneath the main claw on the second.

comb, and the claws of the first and second are sharper and more curved than those of the others. The greater part of the lower side of the digits and of the webs is naked, but the proximal ends of the digits and of the webs is thickly granular like the rest of the sole back to the heel. The greater part of the metatarsal area is covered with a big pad extending on the outer side almost as far as the base of the fifth digit, and on the inner side about halfway between the heel and the hallux, where its edge turns obliquely across the sole to meet the outer edge in a widely-rounded curve. This pad is widest across its middle, gradually and slightly narrowed behind and greatly narrowed in front. Between it and the base of the hallux, and separated from it by a narrower or wider furrow, lies a second much smaller pad, the outer edge of which forms the margin of the metatarsal area in front of the inner portion of the larger pad. The distal third of the smaller pad is at the base of the hallux. In front of these pads the skin is folded and grooved, but shows no definite trace of plantar pads. It is difficult to homologize the two pads above described with the pads on the sole of the hind foot in the Sciuridæ. Tentatively I adopt the hypothesis that the smaller inner pad represents the inner or hallucal element of the plantar pad, which is often large in the Sciuridæ, and that the larger pad represents the two normal metatarsal pads fused together and blended with the rest of the integument. The disappearance of the main elements of the plantar pads in *Castor* is in keeping with their partial or complete suppression in other fully web-footed aquatic forms like the Coypu and some others; and the retention of the pads on the metatarsus is to be explained by the beaver's habit of walking on its heels when carrying objects on land. Whether the above suggested explanation be true or not, it is evident that in the structure of its fore and hind feet the Beaver differs greatly from the Squirrels. (Text-fig. 58, B, C.)

My description of the feet was taken from the European species, *Castor fiber*. The American species has similar feet.

Miller's description of the feet of the European species differs materially from mine. The fore foot, according to him, has five palmar tubercles, "the three at bases of median digits large, ill-defined, that at base of thumb not so large as the others but better defined, its outer surface tending to become smooth and horny, the posterior pad largest, covering about one-third of entire palmar surface." It seems clear from this that the inner of the three above-mentioned tubercles at the base of the pollex is the horny grooved pad I identify as the inner carpal pad. If Miller's interpretation is correct, this is the pollical or inner element of the plantar pad. His "posterior pad" must be the large pad I describe as the outer carpal pad.

In his description of the hind foot it is evident Miller has made the mistake of confusing the first with the fifth digits, for he speaks of the double claw as being on the fourth, whereas it is well known to be on the second digit [*]. This makes his description of the proportionate lengths of the digits (and the sizes of their claws) different from mine. Of the pads he says:—"Three elongate ill-defined pads at base of median digits, a larger and better-defined tubercle behind base of hallux [= fifth digit]; entire sole between hallucal tubercle and heel thickened and pad-like.'

The characters of the principal types of feet in the Sciuromorpha may be tabulated as follows:—

a. Fore foot with well-developed pollex, lobes of plantar pads reduced to folds of flexible integument, carpal pads very large, no carpal vibrissæ; hind feet with all the digits very long, widely separable and united by webs up to the digital pads; lobes of plantar pad mostly obsolete, greater part of metatarsal area covered by one large pad.............................. *Castoridæ*.

a′. Fore foot with pollex reduced to a mere excrescence or absent; lobes of plantar pads well developed, and as prominent as carpal pads, carpal vibrissæ always present; hind foot with shorter digits, free from webs; plantar pad well developed; metatarsus typically with two pads, a longer inner and a smaller outer, both sometimes suppressed

  b. A carpal rod supporting patagium, digits as in arboreal Sciuridæ .... *Petauristidæ*.

  b′. No carpal rod.

    c. Fourth digit the longest, much longer than the second.. *Sciuridæ* (arboreal).

    c′. Third digit the longest, fourth not much longer than second .... *Sciuridæ* (terrestrial).

The Anus and External Genitalia.

In the Sciuridæ and Petauristidæ the anus and external genitalia are normally separated. In the male the prepuce [†] is prominent and situated some distance in advance of the anus, being mostly long and pendulous and even retroverted, when at rest, in the arboreal Squirrels, the Bristly-Ground Squirrels, and the Flying Squirrels, but shorter in the Marmots. Between it and the anus there is in the Squirrels a very large scrotum in the breeding season, but I have not been able to verify this in the case of the Marmots. In the female the vulva is a semicircular or pointed process, situated a little below the anus, and the clitoris is concealed within the labia. The anus has the two normal glands in the Squirrels, whereas in the Marmots there is an additional median gland. (Text-fig. 59, A, B, C.)

The anus and external genitalia in Castoridæ differ profoundly from those of the Sciuridæ and Petauristidæ.

Externally the male and female are alike, owing to the orifices of the alimentary canal and of the genito-urinary organs discharging into a common chamber or cloaca, the aperture of which, closed by a sphincter muscle, is placed at the base of the thick hairy portion of the tail. In the male, moreover, there is no scrotum, the testes being inguinal in position, that is to say, beneath the integument covering the pubic portion of the pelvis. (Text-fig. 59, D.)

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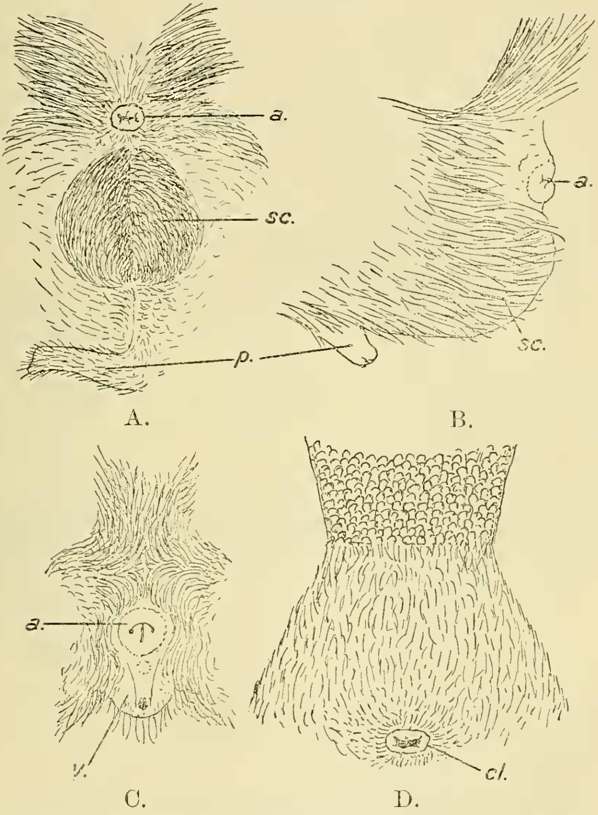
[*] This error no doubt arose from the fashion now in vogue of twisting the hind feet in made-up skins so that the hallux lies on the outer side of the foot so placed.

[†] The structure of the penis and *baculum* I must leave for another paper.

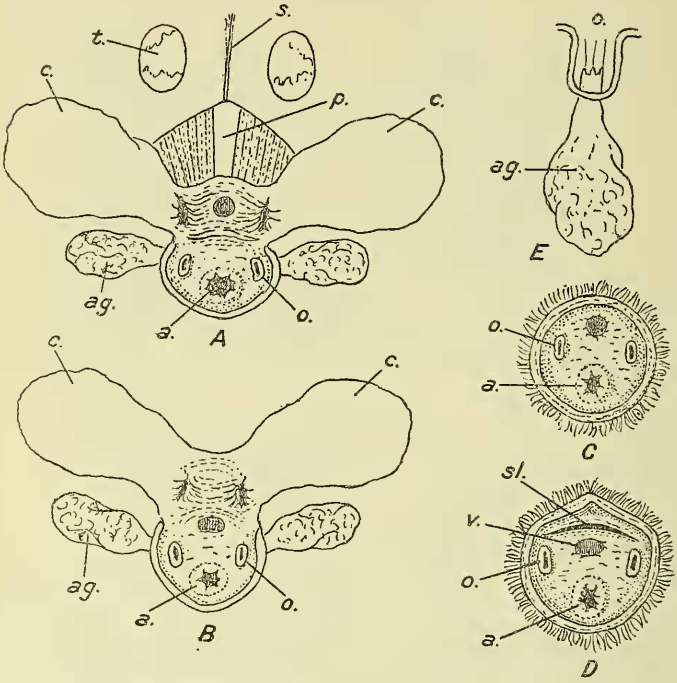
Text-figure 59.



A. Anal and genital region of male of *Callosciurus prevosti*, from below.
B. The same of *Geosciurus capensis*, from the side.
C. „ „ „ female *Cynomys ludovicianus*.
D. „ „ „ male or female *Castor fiber*.
a, anus; *sc*, scrotum; *p*, prepuce; *v*, vulva; *cl*, orifice of cloaca in *Castor*.

When the cloaca of the male is opened, four orifices, two median and one on each side, are seen to open into it. The posterior and larger median orifice is the anus, the anterior and smaller median orifice is the common aperture of the penis and the castorium glands. The paired orifices, one on each side and remote from the anus, are the apertures of the anal glands. Each of the apertures of the anal glands leads into a deep narrow pouch, at the bottom of which are three papillæ, each tipped with a long hair. This pouch can be evaginated, so that the gland comes to the surface, and the strong-smelling secretion is discharged at the tips of the papillæ. Normally the penis is completely retracted, but it is capable of being protruded through the orifice above mentioned into the cloaca and thence to the exterior. Through this orifice the secretion of the castorium

Text-figure 60.



A. Diagrammatic dissection of the anus and genitalia of male *Castor canadensis*.
B. The same of the female.
C. The cloaca of the male, opened.
D. ,, ,, ,, ,, female ,,
E. One of the anal glands, showing the tip with its papillæ and setæ within the pouch.

t, testis; *s*, pubic suture; *p*, penis; *c*, castorium glands with orifices on each side of preputial orifice in male and above vaginal orifice in female; *v*, vaginal orifice; *ag*, anal gland; *o*, orifice of anal gland; *a*, anus; *sl*, slit through which secretion of castorium glands is discharged into cloaca in female.

glands is also discharged. These are represented by a pair of immense sacs, with puckered walls, one lying on each side. They are filled with fluid; and the aperture of each sac opens close to the median aperture of the penis, the three apertures lying close together just within the common orifice above mentioned. (Text-fig. 60, A, C, E.)

The arrangement is very similar in the female, in which the anal and castorium glands appear to be as well developed as in the male. The chief difference is that the orifice of the vagina opens separately into the cloaca. Just in front of it there is a transverse slit in the wall of the cloaca, and when this is opened the apertures of the castorium glands may be seen on each side of it, just in front of that of the vagina. (Text-fig. 60, B, D.)

To sum up, the Castoridæ differ from the Sciuridæ, so far as the organs just described are concerned, in the following particulars:—(1) In both sexes the anus and genitalia open into a common chamber or cloaca with a single external orifice. (2) The anal glands are of great size and open apart from the anus. (3) There is a pair of large castorium glands opening close to the generative orifice. (4) In the male there is no scrotum; the penis is straight and is protruded close to the anus.

In view of these well-known and profound differences, it is singular that in the current text-books the Castoridæ are separated from the Sciuridæ merely by such comparatively trivial differences as are presented by the skull and teeth, the webbed hind feet and broad tail being added as of secondary value, and no mention whatever being made of the genitalia and anus. The difference between the Beavers and Squirrels in the anus and external genitalia may be summarized as follows*:—

a. Sexes externally alike owing to the anus and genito-urinary orifices opening into a cloaca with a single aperture at the root of the tail, no hairy prepuce or vulva, the concealed orifice of the penis just in front of the anus; testes inguinal; a voluminous "castorium" gland opening close to the orifice of the penis and vulva; anal glands very large, with long tubular orifice......... *Castoridæ.*

b. Sexes externally unlike, the anus and external genitalia not opening into a cloaca; female with hairy vulva close beneath anus; male with long perineal region, typically with large scrotum for testes in breeding season; penis long, opening by prominent hairy prepuce on posterior part of abdomen; no "castorium" gland; anal glands small, with small orifice. *Sciuridæ, Petauristidæ.*

From the above-given analyses of the external characters of the Castoridæ, Sciuridæ, and Petauristidæ it will be seen that, so far as the organs considered are concerned, there is not a particle of evidence of kinship between the Castoridæ and the other two families.

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* I have not in this paper dealt with the great differences between the Beavers and Squirrels in the tail, because they are well known.

If the structural differences between the Flying Squirrels and the less specialised true Squirrels entitle these groups to be regarded as distinct families, the differences between the Beavers and the Squirrels must be granted much higher rank. The Sciuridæ and Petauristidæ may be associated as the Sciuroidea, and the Beavers kept apart as the Castoroidea. The Petauristidæ are a compact group represented by several genera and subgenera; but, so far as my limited observations on the external characters are concerned, I have found no reasons for thinking them susceptible of grouping under headings of subfamily rank. The genera of Sciuridæ are much more varied; but their affinities are at present too little understood to warrant the subdivision of the family.